Tansley insight

A hundred years after: endodormancy and the chilling requirement in subtropical trees

Authors for correspondence:
Rishikesh P. Bhalerao
Email: rishi.bhalerao@slu.se

Rui Zhang
Email: rui.zhang@zafu.edu.cn

Received: *3 February 2021*
Accepted: *16 March 2021*

Pawan Kumar Jewaria[1]*, Heikki Hänninen[2]*, Xiaojuan Li[1], Rishikesh P. Bhalerao[1,3] and Rui Zhang[2]

[1]Beijing Advanced Innovation Center for Tree Breeding by Molecular Design, Beijing Forestry University, Beijing, 10083, China; [2]State Key Laboratory of Subtropical Silviculture, Zhejiang A&F University, Hangzhou, 311300, China; [3]Department of Forest Genetics and Plant Physiology, SLU, Umeå S-901 83, Sweden

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New Phytologist (2021) **231:** 565–570
doi: 10.1111/nph.17382

Key words: chilling requirement, climatic adaptation, plasmodesmata, process-based modelling, subtropical trees.

Summary

Endodormancy and the related chilling requirement synchronize the seasonal development of trees from the boreal and temperate regions under the climatic conditions prevailing at their native growing sites. The phenomenon of endodormancy has been known at the whole-plant level for 100 years, and in the last couple of decades, insights into the physiological and molecular basis of endodormancy and its release have also been obtained. Intriguingly, recent studies have shown experimentally that subtropical trees also show endodormancy and a chilling requirement. Motivated by the climatic differences between the subtropical and more northern zones, here we address the similarities and differences in endodormancy between trees growing in the subtropical zone and those growing in more northern zones.

I. Introduction

Perennial plants display annual cycles of growth, which are designed to cope with nonoptimal conditions that accompany changes of seasons. In boreal and temperate regions, these plants cease growth and enclose the shoot apical meristem and leaf primordia within a specialized bud structure. Concurrently with growth cessation and bud formation, a multitude of changes occur at the cellular level, promoting the acquisition of tolerance to low temperatures and shifts in metabolism, which result in the accumulation of storage compounds that can be subsequently utilized for growth in subsequent seasons (Singh *et al.*, 2017).

In addition, one of the most critical transitions that occur in the bud tissues is the developmental transition to endodormancy. Endodormancy can be defined as a physiological state of the bud in which growth resumption is prevented even under growth-permitting environmental conditions (Singh *et al.*, 2017). More recently, Vimont *et al.* (2019) attempted to define molecular markers for endodormancy in *Prunus avium* by modelling gene expression, thus complementing earlier physiological studies. Establishment of the endodormant state plays a key role in the survival of perennating organs as it prevents untimely reactivation

*These authors contributed equally to this work.

of growth (e.g. by unseasonal exposure to growth-promoting conditions in autumn/early winter) until the return of favourable growth conditions in the spring. Release of endodormancy is promoted by exposure to extended periods of low temperatures. In boreal and temperate plants, 4–8°C is typically considered optimal for inducing endodormancy release. This chilling requirement was previously found by Coville (1920), and since then it has been addressed in numerous studies, with both horticultural crops and forest trees (Fuchigami *et al.,* 1982; Hänninen, 2016). Quite surprisingly, it took about 100 years before Du *et al.* (2019) and Song *et al.* (2020) first addressed this research topic with regard to the subtropical zone. They showed experimentally that the 37 subtropical woody plant species they examined also show endodormancy and a chilling requirement. Importantly, this observation now raises the question of whether the mechanism and the regulatory cues of endodormancy have been conserved in evolution or whether distinct mechanisms, implying at least partially different regulatory cues, have evolved in subtropical and in temperate/boreal trees, as the climatic conditions in the native growing sites of these trees differ drastically. Addressing this question is the aim of this review.

II. Peculiarities of endodormancy in subtropical trees

From studies addressing endodormancy, it emerges that endodormancy and its environmental control in subtropical trees differ quite drastically from those of the trees in boreal/temperate regions. The ultimate evolutionary reason for these differences is obviously the distinct climatic conditions specific to these climatic zones (Fig. 1a). Winter is shorter and warmer in the subtropical than in the boreal and temperate regions. This explains why subtropical trees appear to have a relatively shallow endodormancy (Zhang *et al.,* 2021a) and a small chilling requirement (Du *et al.,* 2019) in comparison with those of boreal and temperate trees (Fig. 1c).

On the basis of a climatological comparison, Zhang *et al.* (2021a) concluded that the optimal chilling temperatures of 4–8°C typical for boreal and temperate trees occur infrequently and irregularly in the subtropics. Hence it is unlikely that conditions typically causing endodormancy release in temperate plants at higher latitudes can provide a reliable environmental cue for the progress of autumn in subtropical plants. Accordingly, Zhang *et al.* (2021a) found that temperatures of up to +15°C are effective for endodormancy release in trees of the northern part of the subtropical zone in southeastern China. This is a significant departure from the typical 4–8°C temperatures causing endodormancy release in temperate trees (Fig. 1c). Importantly, with the exception of adult *Torreya grandis* trees, the upper threshold of the endodormancy-releasing temperature range was not even met by the highest chilling temperature of +15°C applied in the experiments of Zhang *et al.* (2021a). Together, these observations led Zhang *et al.* (2021a) to hypothesize that in each climatic zone, temperatures occurring frequently in autumn are effective in the endodormancy release of trees native to the zone. Accordingly, temperature conditions defined as seasonal cues for endodormancy release in temperate trees are not universal for endodormancy release irrespective of the geographical location.

No such climatological comparison as was carried out by Zhang *et al.* (2021a) for the boreal vs the subtropical zone has been carried out to compare different parts of the subtropical zone along a north–south transect. However, the large temperature difference between Hangzhou and Guangzhou (Fig. 1a) suggests that in order for 'chilling' temperatures to provide a reliable seasonal cue for trees under the near-tropical conditions in Guanzhou, the upper threshold for 'chilling' temperatures should be much higher than the +14°C found for Hangzhou in the climatological analysis of Zhang *et al.* (2021a). This suggests that trees native to the low-latitude edge of the subtropical zone may not have endodormancy at all or, if they do, its release is regulated by environmental factors other than air temperature (Fig. 1c). This hypothesis finds indirect support in the artificial selection involved in breeding cultivars of temperate horticultural species to be grown in subtropical and tropical conditions: in these warm climates, only cultivars with low chilling requirements have been found to be productive (Erez, 2000). Together with the experimental findings discussed in the preceding paragraph, these inferences suggest a major difference in the ecophysiology of trees between different parts of the subtropical region. In regions located at relatively high latitudes, the endodormancy phenomena seem to be somewhat similar to those in temperate trees, but in regions located at lower latitudes near the edge to the tropical zone, the endodormancy phenomena, if any, are evidently quite different (Fig. 1c).

However, a low temperature is not the only cue controlling endodormancy release: in several boreal and temperate species, long photoperiod has been shown to act as such a cue as well (Basler & Körner, 2012; Fu *et al.,* 2019). In line with this, Zhang *et al.* (2021b) suggested that the effect of photoperiod in regulating endodormancy release may be more marked in subtropical than in boreal and temperate trees (Fig. 1c). Accordingly, they proposed that photoperiod may regulate endodormancy release and the subsequent ontogenetic development towards leafout and flowering in two different ways. First, long photoperiods prevailing in spring may compensate for lack of chilling. This phenomenon is well documented for many boreal and temperate trees (Worrall & Mergen, 1967; Caffarra & Donnelly, 2011), but under the limited chilling accumulation in the conditions of warm and short subtropical winters, its role may be critical. Second, as an opposite effect, short photoperiods may prevent premature leafout and flowering ('false spring') in warm periods with daily maximum temperatures of +20°C, which often occur in subtropical winters. However, the role of photoperiod as an environmental cue in the subtropical zone may be constrained by the relatively limited seasonal variation of photoperiod in subtropical conditions (Fig. 1b).

III. Process-based modelling of tree phenology in subtropical trees

Since the 1970s, process-based models of tree phenology have been developed for boreal and temperate trees (Hänninen, 2016; Chuine & Régnière, 2017). With air temperature and sometimes photoperiod as their input, these models simulate endodormancy release and the ontogenetic development towards leafout and

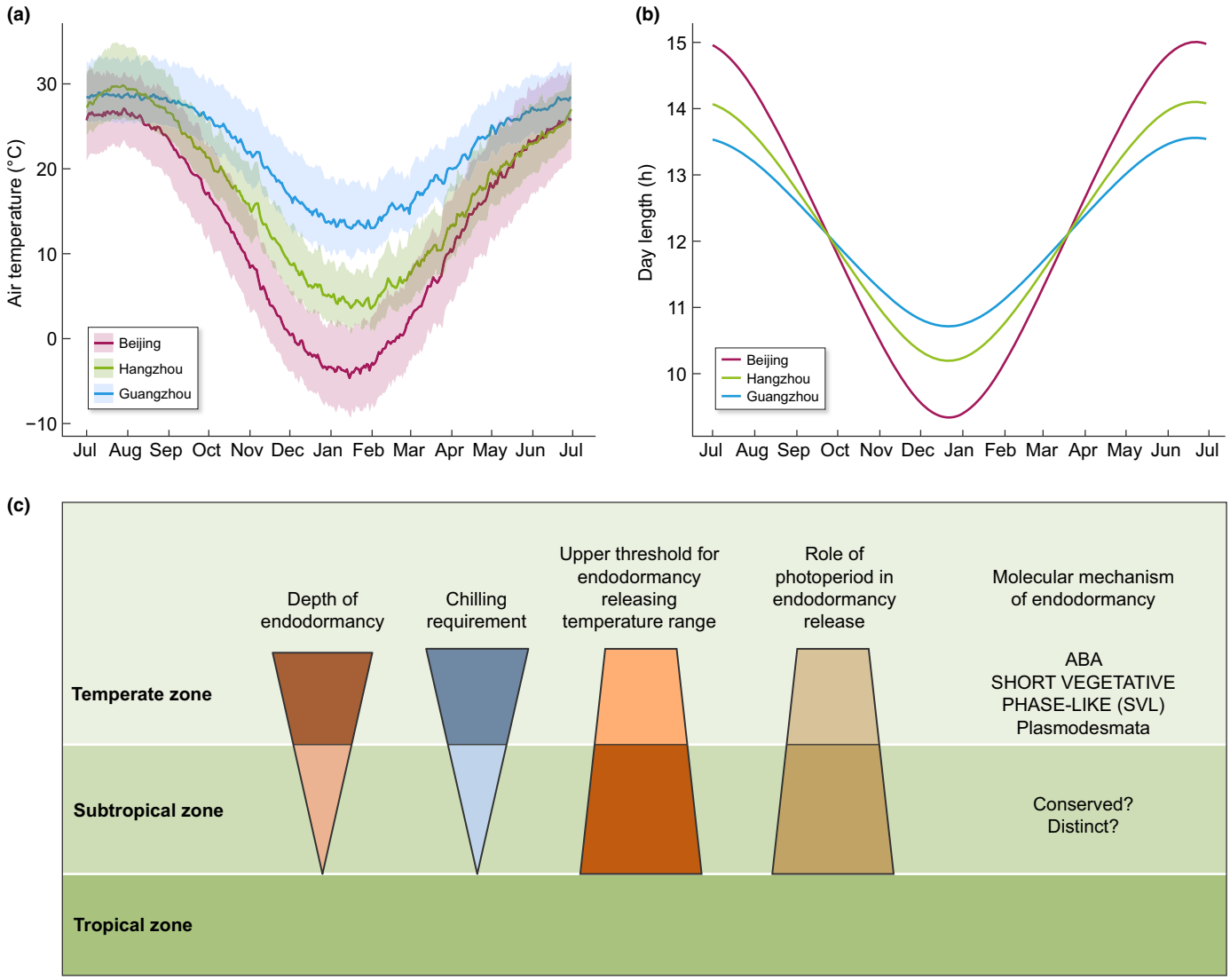

Fig. 1 A conceptual model suggested for endodormancy in buds of subtropical trees, presented in comparison with the same phenomena and traits established for temperate (and boreal) trees over 100 years. Seasonality of (a) air temperature and (b) photoperiod at three locations on a north–south transect in eastern China. The three locations represent the temperate zone (Beijing, 39°54′N, 116°24′E), and the northern (Hangzhou, 30°14′N, 120°1′E) and southern (Guangzhou, 23°6′N, 113°15′E) part of the subtropical zone. In (a), the curve and the lower and the upper end of the shaded area indicate the year-to-year average, minimum and maximum value of daily mean temperature, respectively. The air temperature data were collected by the China Meteorological Administration (http://data.cma.cn) over the years 1958–2018. (c) Suggested changes in tree traits along such transects from the temperate zone at high latitudes to the subtropical zone at low latitudes. The conceptual model is based on the findings of Du *et al*. (2019), Song *et al*. (2020), Xu *et al*. (2020) and Zhang *et al*. (2021a,b).

flowering, providing the dates of these spring phenological events as the final output. In recent decades, process-based tree phenology models have frequently been applied in studies assessing the ecological effect of climatic change (Cannell, 1985; Kramer, 1994; Chuine *et al.*, 2016).

Application of process-based tree phenology models to subtropical trees was initiated only recently by Chen *et al.* (2017), who developed process-based models for *Melia azedarach*, a tree species of tropical origin, and used the models to project the effects of climatic warming on the timing of leafout and flowering in *Melia*. They found that since reduced chilling slowed down the endodormancy release, climatic warming delayed leafout and flowering in the spring. This phenomenon, first suggested by Murray *et al.*, (1989), has been addressed recently in several studies of temperate trees (Fu *et al.*, 2015; Ford *et al.*, 2016; Wang *et al.*, 2020). It should be noted, however, that the model development by Chen *et al.* (2017) was based on the technique of inverse modelling, an approach in which process-based models are fitted to observational long-term phenological records. It has been known since the pioneering study by Hunter & Lechowicz (1992) that this method involves an exceptionally high degree of uncertainty and that biologically unrealistic models are quite often obtained with it (for a recent discussion, see Hänninen *et al.*, 2019). Unfortunately, such was the case in the study by Chen *et al.* (2017), too (for details, see

Zhang *et al.,* 2021c). An observational approach was also taken by Xu *et al.* (2020), who modelled the chilling and heat requirements of four tree species growing in temperate and subtropical regions of China. However, rather than applying inverse modelling, Xu *et al.* (2020) used air temperature responses of chilling accumulation and heat accumulation fixed a priori (Häkkinen *et al.,* 1998). Their modelling results support the notion that the tree species examined also show endodormancy and a chilling requirement of endodormancy release.

Zhang *et al.* (2021c) were the first to develop process-based tree phenology models for subtropical tree species on the basis of results of experiments explicitly addressing the processes modelled. In each case, they projected an advancement of tree spring phenology for the four subtropical tree species examined. For leafout in seedlings, advancing rates were found that were similar to those found earlier for temperate and boreal trees. For *Torreya grandis* flowering, however, the advancing rates were considerably lower, especially in the scenario that assumed strong warming. These differences in the computer simulations addressing the effects of climate change were explained by respective differences in the experimental results among the species and life stages. This shows that to achieve robust projections of the effects of climate change on tree spring phenology in subtropical conditions, experimental research specifically designed to address the dormancy phenomena in subtropical trees is urgently needed.

IV. Plausible endodormancy mechanisms in subtropical trees

The molecular mechanism and the signalling pathway underlying the establishment of endodormancy have been intensively studied in several forest and fruit trees, such as hybrid aspen, grape, peach, apple and kiwi fruit amongst others (Singh *et al.,* 2017; Beauvieux *et al.,* 2018). The key findings from these studies are the central roles of ABA (Zheng *et al.,* 2015; Tylewicz *et al.,* 2018), and the transcription factors of the SVP-related MADS-box family in the regulation of dormancy (Singh *et al.,* 2019; Yamane *et al.,* 2019). Extensive functional analyses of these components in hybrid aspen have shown that the sensing of growth-restricting day lengths (often referred to as short days) enhances the response to the plant growth regulator ABA (Tylewicz *et al.,* 2018). ABA acts via the transcription factor SHORT VEGETATIVE PHASE-LIKE (SVL) to plug plasmodesmata with callosic dormancy sphincters (Singh *et al.,* 2019). The finding that ABA-insensitive hybrid aspen plants that fail to block plasmodesmata also lack endodormancy is a strong indication that blockage of plasmodesmata is an integral part of the endodormancy mechanism (Tylewicz *et al.,* 2018). Importantly, ABA-insensitive plants that lack endodormancy also fail to survive the winter when grown under natural conditions (Yu *et al.,* 2019), highlighting endodormancy as an important adaptive mechanism.

Exposure to a low temperature and the release of endodormancy coincide with the opening of plasmodesmata. However, definitive evidence for the requirement of opening of plasmodesmata and the way it contributes to endodormancy release is still lacking (Singh *et al.,* 2017). In addition, low temperatures are known to induce the expression of FLOWERING LOCUS T (FT), a tree orthologue of the *Arabidopsis* flowering-time gene, and to upregulate the expression of gibberellin (GA) biosynthesis-related genes (Rinne *et al.,* 2011; Singh *et al.,* 2019). It has been shown that FT in trees is required for sustaining growth under long days (Böhlenius *et al.,* 2006; Tylewicz *et al.,* 2015; Miskolczi *et al.,* 2019). Thus, chilling could induce the release of endodormancy and simultaneously promote the activation of growth-promoting signals.

Given the specific attributes of endodormancy in subtropical trees, it might be worthwhile to investigate whether the molecular mechanisms defined for endodormancy release in temperate trees could be applicable to subtropical trees. The simplest explanation for endodormancy release in subtropical trees could be that the optimal dormancy-releasing temperature is higher than that in boreal and temperate trees (Fig. 1c). This would be in line with earlier observations of vernalization. For example, vernalization is typically assayed at 4–8°C in model plants such as *Arabidopsis* (Bastow *et al.,* 2004). However, recent reports suggest that certain genotypes of wheat could achieve vernalization at much higher temperatures, such as 13–18°C (Dixon *et al.,* 2019). While vernalization-mediated promotion of flowering arguably differs from dormancy release, these recent results nevertheless demonstrate that a broad range of temperature signals can be effective in controlling developmental transitions. Whether this is the case for endodormancy regulation in subtropical plants remains to be investigated. An alternative possibility is that a signal other than temperature, such as photoperiod, could act as a seasonal cue releasing endodormancy as discussed above (Fig. 1c). In both cases, an assumption is made that the molecular components of the endodormancy release pathway are conserved during evolution, so that the same mechanisms are found in both boreal/temperate and subtropical trees. However, the alternative hypothesis, namely that the processes of endodormancy regulation in subtropical trees are fundamentally distinct from those in boreal and temperate trees, cannot be excluded (Fig. 1c).

V. Concluding remarks

The few studies of bud endodormancy carried out with subtropical trees at the whole-tree level so far show that results obtained with boreal and temperate trees cannot be generalized to subtropical trees in assessments of the effects of climate change on spring phenology. Rather, species-specific experimental studies and modelling are called for. Similarly, to ascertain which of the above hypotheses of the molecular mechanisms of endodormancy release (Fig. 1c) is valid requires identification of the molecular components that mediate endodormancy, particularly in subtropical trees. Approaches such as those taken by Vimont *et al.* (2019) to define molecular markers for endodormancy by means of gene expression can be helpful in nonmodel subtropical species. The establishment of *Populus* as a model for boreal trees has significantly advanced our understanding of the control of the growth cycle by seasonal cues in boreal and temperate trees. These advances have been aided by complementing the extensive physiological studies with the identification of genetic pathways with functional analyses using transgenic approaches. In the future, a similar approach could set the stage for understanding the molecular basis of endodormancy

in subtropical trees by combining extensive physiological studies with the development of a good model amenable to genetic transformation and obtaining genomics resources, such as a full genome sequence, of a few subtropical trees.

Acknowledgements

The study was financed by The Chinese National Natural Science Foundation (31800579), The National Forestry and Grassland Technological Innovation Program for Young TopNotch Talents (2020132604). PKJ, XL and RPB were funded by financial support from Beijing Advanced Innovation Center for Tree Breeding by Molecular Design and by grants to XL from Beijing Forestry University Outstanding Young Talent Cultivation Project (2019JQ03003). We thank Pekka Hirvonen (www.toisinsanoen.eu) for revising the text. We apologise to our colleagues whose work could not be cited due to limitations in the number of references.

ORCID

Rishikesh P. Bhalerao https://orcid.org/0000-0003-4384-7036
Heikki Hänninen https://orcid.org/0000-0003-3555-2297
Pawan Kumar Jewaria https://orcid.org/0000-0002-1961-3750
Xiaojuan Li https://orcid.org/0000-0002-9955-2467
Rui Zhang https://orcid.org/0000-0002-7235-505X

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